

Studies on southern Australian abalone (genus *Haliotis*) XVII. A chronology of *H. laevisgata*

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Abstract

The abalone *Haliotis laevisgata* deposits 2 rings yr^{-1} in the spire during the first 4–6 years of life at 11 sites in southern Australia. At two sites it deposits 3 rings yr^{-1} , and at another, 3 rings yr^{-1} for the first 3 years and 2 yr^{-1} in the next 3 years. These rates of ring deposition appear to be dependent on the growth rate; they are not exact for every individual due to individual variation in growth but appear to be a statistical property of the population. The tendency for an integer number of rings to be deposited annually may be related to exogenous cues. Hence at one site where 3 rings yr^{-1} are laid down they are deposited in about June, September and December each year, corresponding to winter, the spawning season and summer. Long term tag recaptures suggest that these rates of deposition persist in older shells but better validation is required. Erosion of the shell causes the loss of rings, and the attack of muricid and polydorid borers causes the deposition of adventitious rings as well as pigmented rings, called brown rings. These complications need to be considered in estimating the age of a shell from ring counts.

Key words: *Haliotis laevisgata*, growth, shell aging, chronology, borers, shell erosion, brown rings.

Introduction

The ability to age an abalone shell provides a powerful tool for stock assessment of abalone fisheries because mortality and growth rates can be readily derived without long and costly field experiments. Hayashi (1955) discovered rings in the abalone shell (which are of simple prismatic structure and have been variously described since as growth lines, dark layers, conchiolin layers or prismatic layers) and proposed their use in aging the shell. Muñoz-Lopez (1976) first applied the technique to Mexican species of abalone and it has now been successfully applied to six species (Prince *et al.* 1988, Erasmus *et al.* 1994, Shepherd *et al.* 1995a,b; Shepherd and Turrubiates 1997, Shepherd and Avalos-Borja 1997, Shepherd and Huchette 1997).

The greenlip abalone, *Haliotis laevisgata* Donovan, is fished commercially in southern Australia and lays down non-pigmented rings in the spire, clearly visible in horizontal shell sections. Occasionally, brown rings, so called because they are darkly pigmented, are also laid down. In this paper we use several independent techniques to estimate the rate of deposition of rings in the spire of the shell of this abalone from a number of sites which were chosen to span the main fishing areas in a range of habitats in southern Australia. We also examine two problems, parasitism of the shell and shell erosion, that confound shell aging in order to determine their effect and significance in aging studies.

Materials and methods

Data collection

Shell samples of *H. laevisgata* were collected from 14 study sites (Fig. 1) where the growth rate of

this abalone had been previously studied (Shepherd and Hearn 1983, Shepherd 1988, Shepherd *et al.* 1992, Wells and Mulvey 1995, unpublished data). Using the techniques described in detail by Shepherd *et al.* (1995b) we took horizontal sections by rasping the spire to expose the rings and counted them under a low power binocular microscope. We discarded shells heavily bored by boring organisms as they were unreadable. For the Taylor Island site we also examined monthly collections of 10–15 adult shells in order to estimate the time of deposition of the rings. The shells were sectioned at the spire as described above to expose the layer of shell (whether a ring or nacre) most recently laid down. Two additional samples of shells grown in culture were examined. The parent broodstock of both samples came from Taylor Island. One sample was grown in a hatchery for 25 months at high final densities of $> 200 \text{ m}^{-2}$, and the other was grown at low densities ($< 20 \text{ m}^{-2}$) for 20 months. We examined samples of shells taken by commercial divers from Hopkins Island and Cathedral Rock in Thorny Passage to determine the relation between the deposition of brown rings

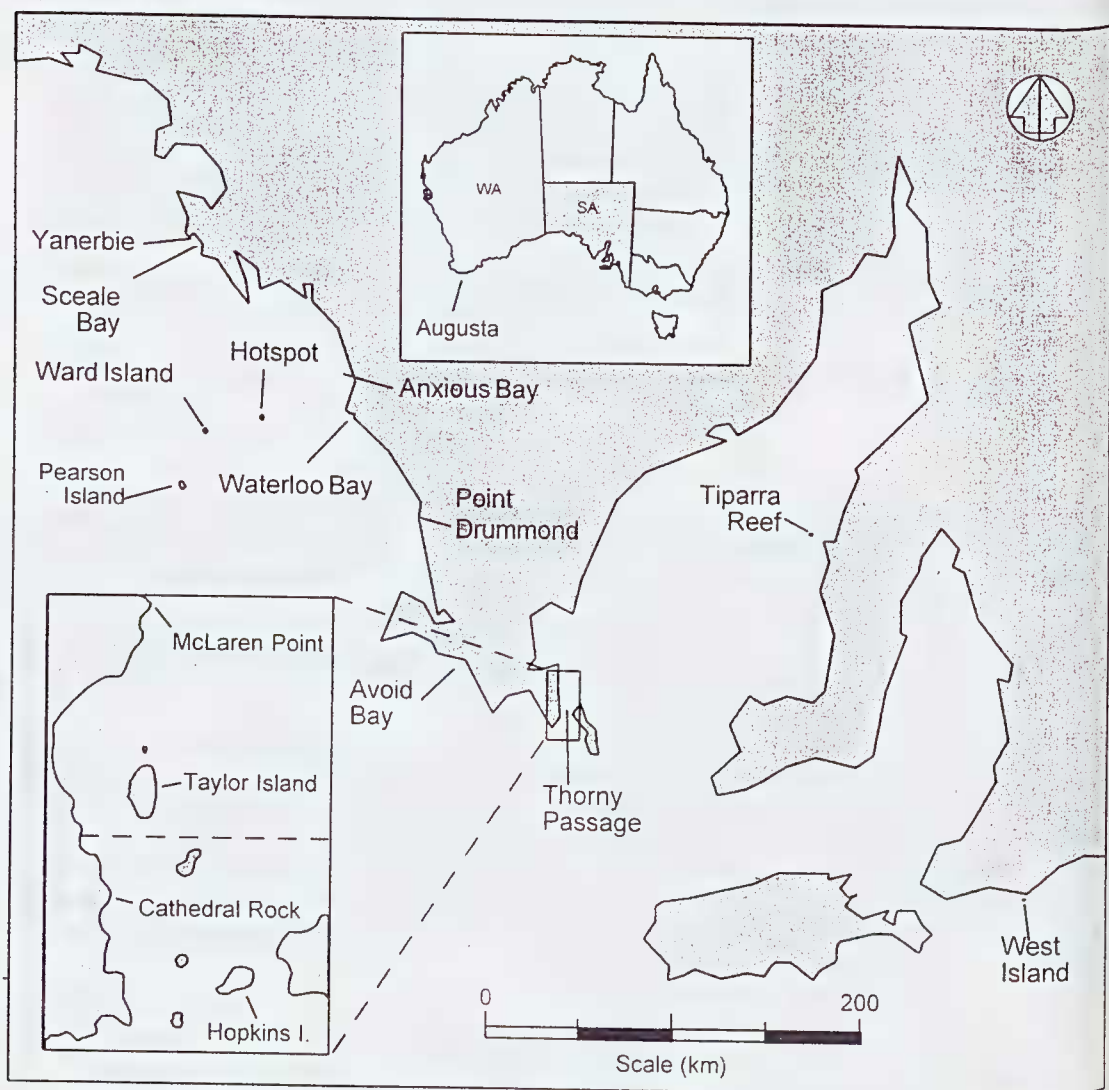


Figure 1. Map of South Australia with insets showing study sites.

(described by Shepherd and Huchette 1997) and drilling of the shell by the muricid snail *Haustrum baileyannum* (Thomas and Day 1995) and boring of the shell by polydorid polychaetes (Shepherd 1973). We categorised shells as slightly bored when < 50% of the sectioned surface area at the spire (about 1 cm²) was intensely perforated by borers and moderately bored when > 50% of the area was infested. Our third category of heavily bored shells was the unreadable ones. We then scored shells for the presence or absence of brown rings in 4 categories of shell: those (a) slightly or (b) moderately bored by polychaetes and (c) with or (d) without muricid drill holes. The presence of drill holes is most easily seen by examining the ventral nacreous surface of the shell where a half pearl of nacreous material is always deposited at the site of the hole; this can then be confirmed by dorsal examination of the shell. To estimate the effect of erosion of the shell and of polychaete boring on the number of extant rings we examined a sample of shells from Sceale Bay where both effects were conspicuous. In eroded shells, commonly known as “shinybacks”, the periostracum is worn away exposing the nacreous layer. We compared the net rate of deposition of rings with size in samples of shinybacks, uneroded shells and bored shells in the size range 100–150 mm shell length (SL).

Statistics

The growth rate of *H. laevis* is linear with age for the first 4–6 years according to site and thereafter is curvilinear. The linear phase can be fitted by a linear regression and the curvilinear phase by a von Bertalanffy growth curve (Shepherd and Hearn 1983; Shepherd 1988; Shepherd *et al.* 1992). Shell length is a good predictor of age in the linear phase but not in the curvilinear phase because of the dependence between the growth parameters K and L'. This can be seen by looking at the derivative with respect to time of the von Bertalanffy equation:

$$L_t = L_{\infty} (1 - e^{-kt})$$

At t=0, L'=L_∞ K i.e., the same slope will be obtained with different values of L_∞ and K. Another difficulty is that during the linear phase the growth rate of individuals varies and the variance of the mean growth rate increases, apparently linearly with length (see discussion in Day and Fleming

Table 1. The sites studied, showing the methods used to estimate growth rates, the length range to which they apply, and the mean growth rates (mm yr⁻¹) during the linear growth phase with authority. Abbreviations: s.e. = standard error; T = tagging studies; CS = growth of cohorts from snapshot data sets.

Site	Method	Length range (mm)	Growth rate (s.e.)	Authority
West Island	T	25–110	20.3 (0.4)	Shepherd (1988)
Tiparra Reef	CS	48–102	20.9 (0.7)	Triantafillos (1994) – 1990 data
McLaren Point	CS	20–140	23.6 (1.1)	Shepherd <i>et al.</i> (1992)
Taylor Island	CS,T	15–145	39.6 (0.9)	Shepherd <i>et al.</i> (1992)
Avoid Bay	T	45–115	19.7 (2.4)	Unpublished 1987 data
	CS		18.1 (0.5)	Unpublished 1995 data
Pt Drummond	CS	10–110	24.7 (2.2)	Huchette (1995)
Pearson Island	CS	50–125	16.9 (0.3)	Huchette (1995)
Ward Island	T	60–125	25.7 (1.5)	Shepherd <i>et al.</i> (1992)
	T		21.3 (2.1)	Revised estimate with more data
	CS		19.4 (2.3)	Unpublished 1986 data
Hotspot	CS	50–120	20.7 (2.6)	Huchette (1995)
Waterloo Bay	CS,T	50–120	20.8 (0.3)	Shepherd and Silveira (in prep.) – 1997 data
Anxious Bay	CS,T	25–95	20.4 (1.5)	Shepherd <i>et al.</i> (1992)
Sceale Bay	CS,T	45–110	20.4 (1.8)	Shepherd <i>et al.</i> (1992)
Yanerbie	CS,T	15–110	15.3 (0.9)	Shepherd <i>et al.</i> (1992)
Augusta, W.A.	T	20–100	31.6 (1.8)	Wells and Mulvey (1995)

1992). This does not invalidate the use of length as a predictor of age but it requires that sample sizes be larger to reduce the variance of the estimated regression slopes. For each site we first obtained a linear regression equation expressing the relation between length and age during the linear phase of growth (Table 1). We used published estimates of the growth rate, or more recent unpublished estimates. For two sites we give more than one estimate, because different methods produced slightly different growth rates or, as at Ward Island, we have more data. In the case of Waterloo Bay, more recent studies suggest a decline in the growth rate possibly due to selective fishing (Shepherd and Silveira in prep.), so we used the most recent estimates. We then regressed the number of rings vs shell length for each site by least squares analysis. By substituting the relation between length and age (Table 1) in these regression equations we derived estimates of the number of rings laid down annually. Standard errors of multiplicands were calculated with formulae from Green and Margerison (1977). The data for McLaren Point showed a change in slope so we fitted a broken stick model i.e., two linear regressions with a visually selected break point. No other data set gave hint of a change in slope.

The statistical power of the regressions to detect a 25% change in slope, at a significance level of $\alpha=0.05$ at the given sample sizes, was calculated with a Statgraphics computer package (Anon. 1986). While an effect size of 50% should be enough to discriminate between deposition rates of integer numbers of rings yr⁻¹ we conservatively chose a 25% level.

In the analysis of the mark-recapture data we used the regression equation derived for the site in question (Table 2) to estimate the number of rings laid down at the date of tagging. This was valid because the recaptured abalone were all marked during the linear phase of growth. We counted the number of rings at the spire at the date of recapture and, by deduction, an estimate of the number of rings laid down during the period at liberty.

Table 2. Regression equations of number of rings (R) vs length in mm (L) for *H. laevis* at 14 sites, with estimates of the number of rings deposited annually and in the first year. N = the number of shells examined. Power is the power to detect a 25% change in the slope at the given sample size. s.e. = standard error.

Site	N	Regression equation	r ²	No. rings yr ⁻¹ (s.e.)	No. rings in 1st yr	Power
West Island	81	R = 0.97 + 0.092L	0.343	1.87 (0.61)	2.8	0.49
Tiparra Reef	32	R = -0.63 + 0.109L	0.779	2.28 (0.22)	1.2	0.79
McLaren Point	63	(a)R = -2.07 + 0.125L	0.772	2.96 (0.25)	0.8	0.99
	88	(b)R = 2.25 + 0.081L	0.510	1.90 (0.22)		0.73
Taylor Island	150	R = 0.30 + 0.079L	0.750	3.14 (0.17)	1.5	0.99
Avoid Bay	60	R = 0.33 + 0.090L	0.793	(1) 1.77 (0.28)	2.0	0.99
				(2) 1.62 (0.17)	2.2	
Pt Drummond	16	R = 1.44 + 0.091L	0.973	2.22 (0.17)	3.3	0.99
Pearson Island	32	R = -1.64 + 0.118L	0.707	1.99 (0.23)	0.4	0.72
Ward Island	58	R = 1.58 + 0.094L	0.628	(1) 2.41 (0.27)	2.3	0.99
				(2) 2.00 (0.28)	2.8	
				(3) 1.82 (0.28)	3.1	
Hotspot	51	R = 0.10 + 0.102L	0.472	1.98 (0.15)	1.9	0.52
Waterloo Bay	60	R = 0.002 + 0.107L	0.764	2.23 (0.17)	2.7	0.95
Anxious Bay	71	R = 0.67 + 0.111L	0.848	2.26 (0.22)	2.1	0.99
Sceale Bay	66	R = 1.42 + 0.089L	0.628	1.82 (0.24)	1.5	0.8
Yanerbie	62	R = -0.37 + 0.124L	0.813	1.90 (0.16)	1.0	0.99
Augusta, W.A.	41	R = -0.38 + 0.099L	0.672	3.14 (0.39)	2.8	0.96

The multiple values for the number of rings yr⁻¹ given for Avoid Bay and Ward Island refer to the multiple growth rates given for those sites in Table 1. The two regression equations for McLaren Point relate to the two parts of the broken stick model.

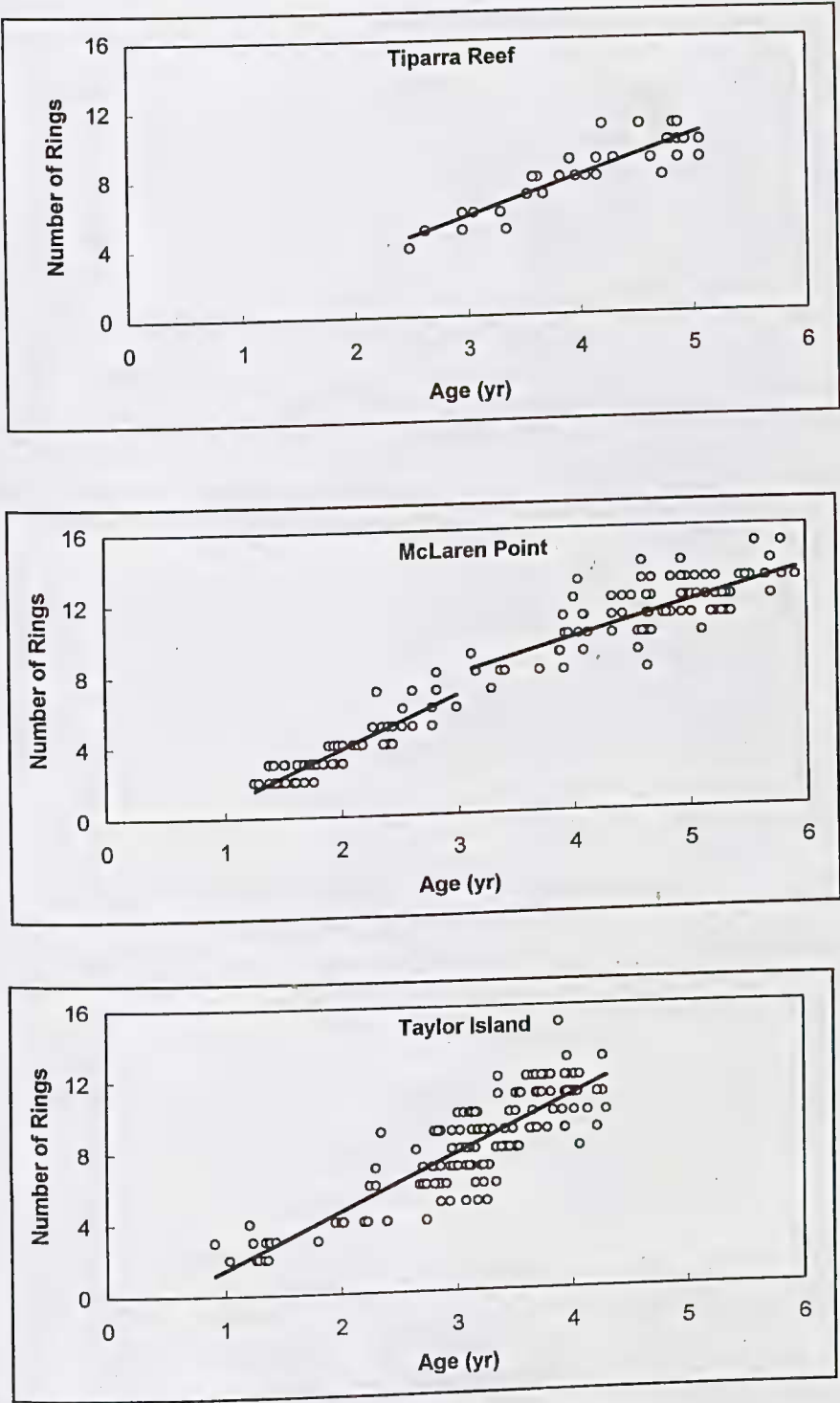


Figure 2. Plots of number of rings vs shell length for three sites showing different patterns of ring deposition: Tiparra Reef (2 rings yr⁻¹), Taylor Island (3 rings yr⁻¹) and McLaren Point (3 then 2 rings yr⁻¹).

Results

Deposition rates

The sites studied, with estimates of the growth rate of *H. laevigata* and authority, are given in Table 1. The regression equations relating the number of rings to shell length, with estimates of the number of rings deposited in the first and subsequent years, are given in Table 2. Plots for three sites illustrating the different patterns of deposition are shown in Fig. 2. The number of rings laid down did not differ significantly from 2 yr⁻¹ at 11 of the sites and 3 yr⁻¹ at two sites. At one other site (McLaren Point) the rate of deposition changed from 3 to 2 yr⁻¹ at about three years of age. The change in slope of the regressions (Fig. 2) was significant ($t=8.0$; $P<0.001$). Although none of the three estimates of rates of ring deposition for Ward Island differed significantly from 2, the last two, based on more or more recent data, are probably more accurate. Statistical power (Table 2) was adequate (0.7-0.99) to detect a change of 25% in the slope of all the regressions except at West Island and Hotspot, but even at these sites it was adequate (>0.9) to detect a 50% change.

Next we examined the probability of deposition of the nearest alternative integer number of rings yr⁻¹ for each site. For example, at West Island our estimate was 1.87 rings yr⁻¹ (Table 2), so we examined the hypothesis of 1 ring yr⁻¹, and rejected it ($t=2.5$; $P<0.02$). Similarly, we rejected the hypotheses of the nearest alternative integer for every other site (in every case $3.1<t<6.7$ and $P<0.001$ except for Ward Island where the nearest alternative for 2.4 rings yr⁻¹ i.e. 3 rings yr⁻¹ was rejected with $t=2.5$, $P<0.05$).

The number of rings laid down in the first year appeared to vary from 1 to 3 according to site (Table 2). However, little confidence can be placed in any of them. The standard errors (not shown) are >1 and in any case the estimates are extrapolations beyond the range of the data. The mean growth rates of the two samples of shells of *H. laevigata* grown in culture differed significantly ($t=8.0$; $P<0.001$) from each other (Fig. 3), and within each sample there was wide variability in growth rate. Although the mean number of rings deposited did not differ significantly from 3 yr⁻¹ for either sample (Table 3), individuals deposited a variable number of rings ranging from 2.3-4.3 yr⁻¹

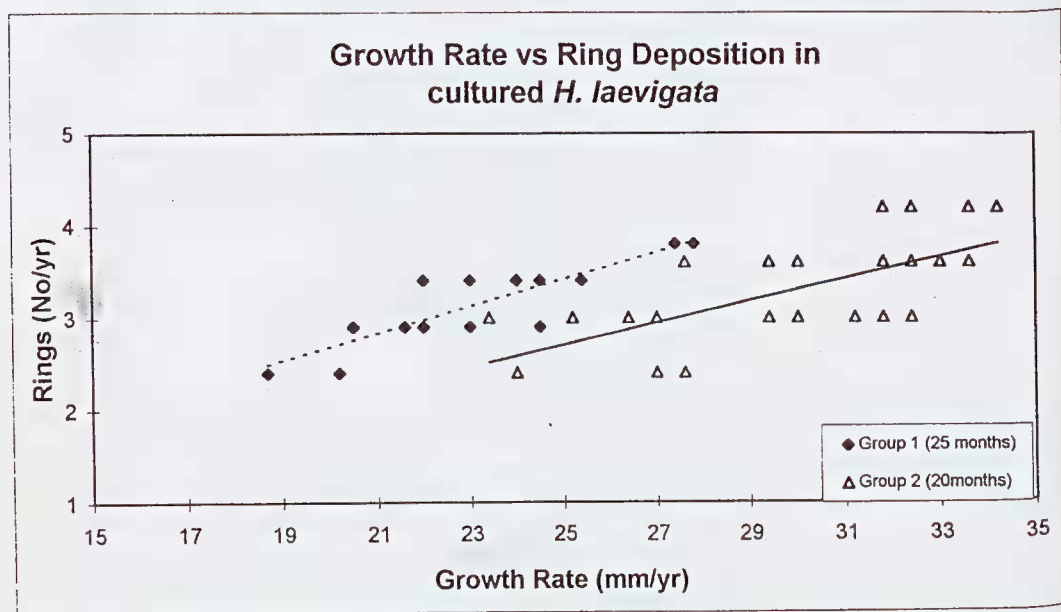


Figure 3. Plots of deposition rate vs growth rate for two samples of shells grown in culture at different growth rates.

Table 3. Rates of deposition of rings in shells of *H. laevis* grown in culture with regression equations of number of rings (R) vs growth rate (GR) in mm yr⁻¹. N = sample size. Both regression slopes were significant: (1) P<0.001; (2) P<0.05.

Sample	Period (mths)	N	Shell lengths (mm)	No. of rings yr ⁻¹	Regression	r ²
(1)	25	19	39–58	3.19 (0.09)	R=-0.26+0.15GR	0.719
(2)	20	29	39–57	3.29 (0.10)	R=-0.27+0.12GR	0.460

(Fig.3). The fractions of rings result from adjustments for the non-integer number of years at liberty. Among individuals in each sample a regression of the number of rings yr⁻¹ vs the growth rate was significant (Table 3, Fig. 3).

In the monthly samples of adult shells (120–160 mm SL) from Taylor Island examined for evidence of time of deposition of rings, a plot of the proportion of the shells with a ring newly laid down vs time (Fig. 4) shows that 90–100% of the samples taken in June, September and December had just deposited a ring. This implies that adult shells, as well as juveniles, deposit about 3 rings annually at this site.

Tagging data

The mark-recapture data for 73 shells (Table 4) show variability in the number of rings laid down between and within sites. Yet 63 of the shells (variously grouped to illustrate points discussed) deposited, on average, very close to 2 or 3 rings annually according to site. At West Island and Tiparra Reef the mean number is 1.9–2.1 for individuals at liberty from 2 to 15 years. At Taylor Island some were marked *in situ* and others removed from the water for tagging in separate experiments. There were no significant differences in the number of rings laid down by the two

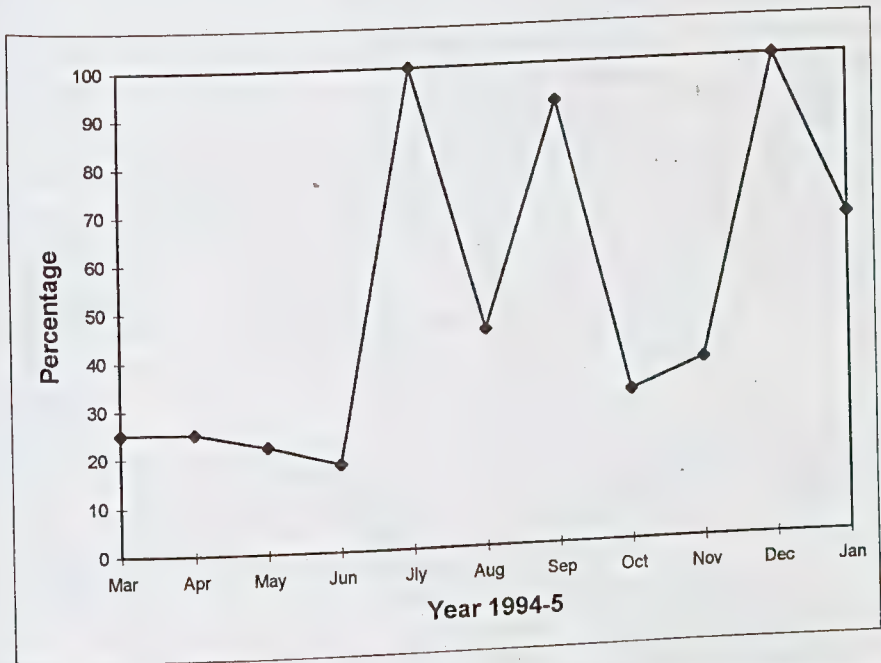


Figure 4. Plot of proportion of shells with a ring newly laid down vs month of collection for samples from Taylor Island.

Table 4. Summary of mark-recapture data for *H. laevigata* at various sites with the estimated number of rings deposited per annum during the period at liberty. Data for West Island, Taylor Island and Waterloo Bay are shown in several groups to illustrate features discussed in the text. N = sample size; Age = estimated age at tagging; Period = mean period at liberty in years (with standard error).

Site	N	Age (s.e.)	Period (yrs)(s.e.)	Rings yr ⁻¹ (s.e.)	Comments
West I.	4	3.1 (0.03)	2.1 (0.6)	1.8 (0.8)	
	2	2.3 (0.4)	2.0 (1.0)	0	Did not grow
	1	3.8	15.3	1.9	
McLaren Point	1	5.5	2.3	0.4	Grew very slowly
Taylor I.	4	2.7 (0.2)	2.1 (0)	4.7 (0.7)	Heavily bored by polydorids
	7	2.4 (0.3)	3.6 (0.4)	2.7 (0.3)	Tagged out of water
	18	2.4 (0.1)	2.1 (0)	2.9 (0.2)	Tagged <i>in situ</i>
	19	2.3 (0.1)	1.3 (0)	2.5 (0.2)	A mean of 3.3 rings laid down over 16 mths
Avoid Bay	1	3.9	5.7	2.1	
Waterloo Bay	7	3.9	1.0 (0)	2.0 (0.3)	
	1	2.9	8.3	1.5	At a site of stunted growth
	1	3.1	8.3	0.9	Shell badly eroded
Anxious Bay	1	2.6	2.5	1.1	At a site of stunted growth
Tiparra Reef	6	5.1 (0.1)	2.0 (0.2)	2.1 (0.4)	Tagged <i>in situ</i>

groups ($t=0.5$; n.s.). A group at liberty for 16 months laid down a mean of 3.3 rings but marking was done in March and no rings are expected to be laid down until about June (Fig. 4) so the uncorrected number (3.3) is probably a better estimate of the mean annual deposition rate for this group. This example shows that where rings are deposited at a specific time of the year then mark-recapture data for individuals at liberty for a non-integer number of years, when adjusted to annual periods, can under- or over-estimate the deposition rate. Four shells recaptured from Taylor I. were parasitised by polydorid parasites. These shells laid down significantly more rings than others marked at the same time and at liberty for the same period ($t=2.7$; $P<0.02$). This could not have been due to their different growth rate because it was slightly, but not significantly, faster than that of the non-parasitised shells. Further, 12.5% of the shells recaptured at Taylor Island showed the deposition of a brown ring at the location in the shell structure where a ring would be expected if it had been laid down at the time of marking.

Six marked individuals, which grew very slowly or not at all, deposited fewer rings than expected. The conspicuously eroded shell (Table 4) may have deposited fewer rings or, more likely, lost some.

Table 5. Relation between the presence of brown rings in the shell and the effect of two kinds of parasites, drilling by *Haustrum* and boring by polychaetes, in *H. laevigata* at Hopkins Island.

Shell characteristics	Brown rings absent	Brown rings present
neither drilled nor bored	58	5
not drilled, but bored	3	30
drilled but not bored	18	46
both drilled and bored	2	22

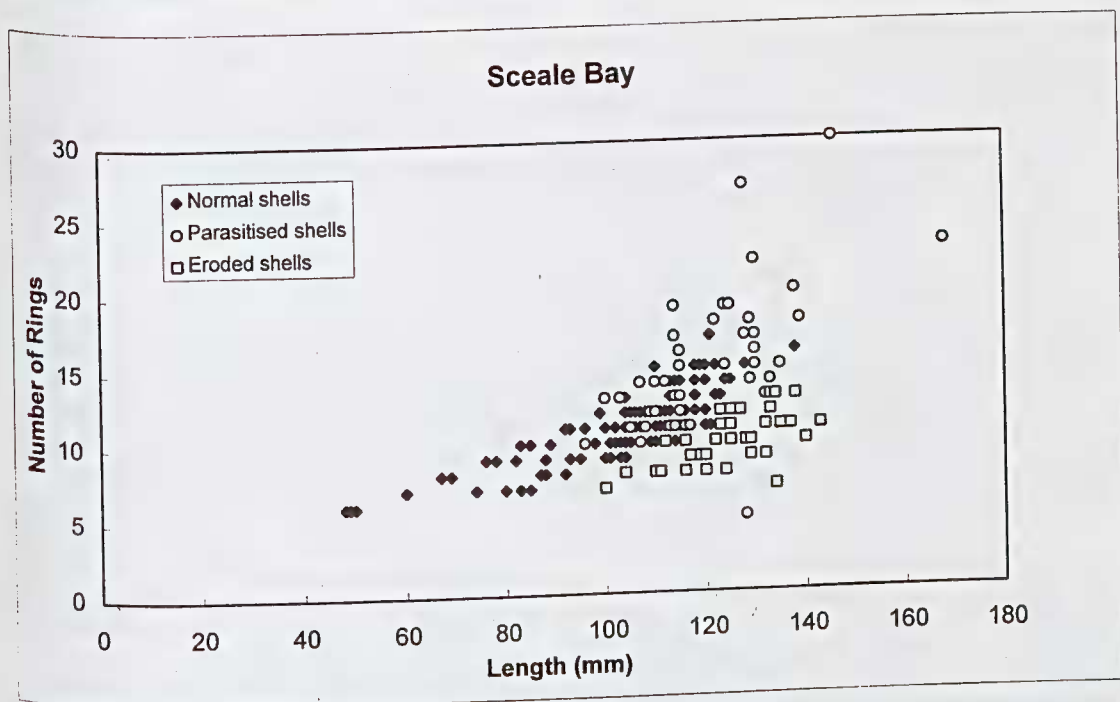


Figure 5. Plot of the number of rings vs shell length for normal, eroded and parasitised shells for a sample of shells from Sceale Bay.

Shell erosion and effect of parasites

At Sceale Bay shells with epizoic limpets were generally eroded whereas shells without these epizoites were overgrown with epizoic algae and were not eroded. Other shells also without these epizoites were bored by polychaetes. A plot of the number of rings vs shell length for a sample of 182 shells (Fig. 5) classified in 3 classes of shell shows that over the size range 45–110 mm SL the number of rings increases linearly with length; the regression equation (Table 2) indicates a deposition rate of about 2 rings yr^{-1} . In larger shells those that are parasitised have more rings than normal shells, and those that are eroded have less. Comparison of regression slopes between the three classes of shells has little meaning because the ranges of the length values, and probably the growth rates, differ between them.

Next we examined the question whether brown rings were caused by parasitic attack in the shell sample from Hopkins I. In all, 56% of the sample had one or more brown rings in the spire although in many cases these were very fine and short and similar to those classified as false rings by Shepherd *et al.* (1995b). The data (Table 5) show that brown rings seldom occur in shells which have not been attacked by parasites and are more likely to be present after parasitic attack. In the 5 examples of brown rings present in unbored and undrilled shells, three of them had prominent growth checks suggesting that some external event had severely affected growth. First we tested the null hypothesis that the presence of brown rings was independent of drilling and boring and rejected it ($\chi^2_4 = 247$; $P < 0.001$). Then we tested the further null hypotheses that the presence of brown rings was independent of (a) muricid drilling of the shell in the absence of boring by polychaetes, and (b) boring by polychaetes in the absence of muricid drilling. We rejected both hypotheses (for drilling $\chi^2_2 = 64.6$; $P < 0.001$; for boring $\chi^2_2 = 53.9$; $P < 0.001$) and concluded that both kinds of parasites independently of each other provoke the deposition of a brown ring by the abalone. The reason why brown rings are more often absent in drilled shells (28%) than in bored shells (9%) may be because we scored for drilling over the whole of the shell but for boring only in the region of the

spire. We noticed that brown rings were larger and more likely to be present when drilling occurred near the spire than when it occurred over the adductor muscle away from the spire. In another sample of commercial shells from Cathedral Rock (data not shown), some 10 km from Hopkins I., 23% of the shells ($N=140$) had brown rings although they were neither drilled nor bored, indicating variability in the rate of deposition of brown rings between sites. Here, too, drilling and boring both caused significant increases in the incidence of brown rings.

Discussion

The two techniques we used to estimate growth rates, mark-recapture data and analysis of 'snapshot' length-frequency data, have generally given consistent results (Shepherd 1988, Shepherd *et al.* 1992). However, differences between them can occur due to biases associated with each (reviewed by Day and Fleming 1992). Hence the multiple growth rate values given for two sites (Table 1) could reflect possible biases. The only large discrepancy was at Ward Island, and the first estimate given in Shepherd *et al.* (1992) was probably improved by the addition of more recapture data reflected in the later estimate.

Earlier studies on the deposition of rings in abalone (Erasmus *et al.* 1994; Shepherd *et al.* 1995a,b) have shown individual variability in the rate of ring deposition, but the cause(s) have not been elucidated. Our study gives some clarification to this issue. Variability has been shown both between and within sites, and in both cases we hypothesise a dependency on the growth rate.

A comparison of sites suggests that, where the mean annual growth rate is in the range 15–23 (–25) mm yr⁻¹, 2 rings yr⁻¹ are laid down, and at sites of faster growth 3 rings yr⁻¹ are laid down. The same transitional growth rate region is evident in Figure 3. The data for McLaren Point is especially interesting because it suggests that a slight reduction in growth rate compared with nearby Taylor Island, as may occur at sexual maturity, can be sufficient to change the pattern. We do not know what happens when growth rates are < 15 mm yr⁻¹, although the recapture data (Table 3) suggest that < 2 rings yr⁻¹ are likely to be laid down.

Within site variation also occurs and our data on rings laid down in cultured shells show that 46–72% of the variation in ring deposition is explained by differences in individual growth rate. Natural variation in growth rate in wild populations of abalone is notoriously high (Day and Fleming 1992), so this may explain much of the variability we have found. For example, the West Island sample shows the highest variability (Table 2), which may reflect the rarity of this abalone there (Shepherd and Brown 1993), and our sampling of several reefs where growth rates differed (Shepherd 1987).

However, our growth-rate dependency hypothesis does not explain why very close to an integer number of rings is apparently laid down annually by this species at every site. If the rate of deposition were wholly dependent on the growth rate we would expect continuous variation rather than a punctuated pattern. So we propose that the deposition of rings may be linked to an exogenous cue such as sea temperature and/or spawning which predisposes this species to deposit 2 or 3 rings yr⁻¹ according to prevailing growth rates. Consistent with this hypothesis, ring deposition of *H. laevis* at Taylor Island is restricted to three specific times of the year (Fig. 4), corresponding with winter and summer temperature extremes and spawning. In two other species of abalone (Shepherd *et al.* 1995b, Shepherd and Huchette 1997) rings are deposited near the time of sea temperature extremes. Erasmus *et al.* (1994) argued that ring deposition was endogenous because a constant number of rings was laid down annually in shells of *H. midae* grown in culture at a constant temperature. This is quite possible because endogenous rhythms may also be linked with exogenous cues (Tevesz and Carter 1980). If ring deposition is related to some stress, as argued by some, then the question arises whether the removal of an abalone from the water for marking might affect the pattern of ring deposition and so cause a bias. Our few data (Table 4) suggests this does not occur, although a brown ring does sometimes seem to be laid down at about the time of tagging whether it is done in or out of the water (see results).

Shell erosion and parasitism

Erosion of the shell is conspicuous in *H. laevis* due to exposure of the nacre and occurs where the abalone lives in a habitat strongly abraded by sand, or in places where the epizoic limpet, *Patelloida nigrosulcata* is common. We have not examined critically the association between them except to observe a correlation between the presence of the limpet and shinyback shells. Wells (1988) describes a similar association between this limpet and *H. roei* in Western Australia. We tentatively suggest that the limpet by its grazing activity either directly abrades the periostracum and nacre with its radula or by removing epizoic, filamentous algae exposes the shell to erosion by sand. Both possibilities may be true. In Scaale Bay about 28% of the shells were shinybacks with epizoic limpets. Only 2 of these (c.1%) also had polychaete parasites so the presence of the limpets may reduce the incidence of parasitism in shells.

The presence of boring polychaetes in the shell and of the epizoic limpet *Patelloida nigrosulcata* was not common at our study sites except at Scaale Bay (Fig. 5). There are two possible explanations for the apparent increase in the rate of deposition of rings in parasitised shells compared with "normal" ones. The irritation may cause the abalone to deposit more rings, as shown by the tagged shells from Taylor I., or alternatively, the growth rate of parasitised shells may be lower as the animal diverts relatively more energy into shell repair than into growth, or both may be true.

Brown rings

Brown rings are much less conspicuous in *H. laevis* than in *H. scalaris* (see discussion in Shepherd and Huchette 1997), so they can be easily overlooked. Our data show that drilling by muricid snails and boring by polychaetes stimulate the production of brown rings and that even the disturbance from tagging may apparently induce their deposition. Thomas and Day (1995) mimicked the drilling of a muricid snail in the shell of *H. rubra* and induced the deposition of a black proteinaceous layer around the hole. This is the same phenomenon.

Brown rings are rich in conchiolin and their presence as adventitious layers deposited in response to shell penetration by foreign bodies or contaminants is well known among molluscs (Tevesz and Carter 1980). Their presence in abalone shells, once recognised and allowed for, does not present a problem for aging.

Use of ring counts for aging shells

The use of ring counts for aging requires that they be laid down with consistent frequency and that biases can be eliminated (Day and Fleming 1992). Our data show that rings do not accurately tell the age of every individual but they should give an unbiased probabilistic age for a population sample. For many sites examined validation has been achieved only for the first four to six years of life during the linear phase of growth. The mark-recapture data and the data on timing of ring deposition (Fig. 4) extend the validation by implication to older age classes, but further validation is still desirable, given the variability we have encountered. It is possible, for example, that the deposition rate could change in older shells as found by Shepherd and Turrubiates (1997) in *H. fulgens*.

Our data show that biases in aging can occur through parasitism of the shell, which leads to over-estimation of age, and erosion of the shell, which leads to under-estimation. Parasitism of the shell by boring polychaetes is a more difficult problem because shells may vary from being mildly to heavily parasitised, and there is an element of subjectivity in deciding when to exclude a shell from aging. The optimal solution here is to classify shells according to the number of rings by the Shepherd and Huchette (1997) and estimate the contribution to the growth rate, so we "parasitism" effect. This, of course, requires a good understanding of the growth rate, so we recommend that shell-aging should be done routinely as a part of mark-recapture studies. It does not follow from this dependency on the growth rate and the consequent variability that aging of the shell *per se* has little use. Once validation is achieved it becomes a valuable tool for deriving an age-length key and for estimating mortality which are otherwise intractable or very costly.

The bias caused by shell erosion seems not to be serious for *H. laevis* except where "shinybacks"

are common. Our studies so far suggest that the phenomenon is restricted to shallow-water populations in the warmer parts of this species' range (unpublished data), and at a few sites where sand abrasion is common.

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